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Research Article

Ecological interactions driving spring dynamics of *Aurelia aurita* medusae (Linnaeus, 1758) in the western and north-western Black Sea

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Abstract

This study examined the ecological factors influencing spring fluctuations in the medusa population of the moon jellyfish (*Aurelia aurita*) in the western and north-western Black Sea between 2009 and 2015. Data were collected at 216 sampling stations, mainly covering coastal and shelf waters of Bulgaria, Romania and Ukraine. The north-western Black Sea exhibited the highest mean abundance (2.48 ind/m^3 ± 0.92 SD) and biomass (4.65 g/m^3 ± 3.22 SD) of *A. aurita*, despite individuals in this region having the smallest mean bell diameter (5.7 cm ± 1.5 SD). In contrast, the western regions (Bulgarian and Romanian waters) showed lower, yet comparable abundance and biomass, with mean values of 1.31 ind/m^3 ± 1.01 SD to 1.33 ind/m^3 ± 1.08 SD and 3.79 g/m^3 ± 3.93 SD to 3.99 g/m^3 ± 3.72 SD, respectively, alongside slightly larger average bell diameters (6.2 cm ± 1.8 SD and 6.3 cm ± 1.7 SD). Generalised Additive Models identified mesozooplankton biomass and sea surface salinity as key predictors of jellyfish biomass, while depth significantly influenced abundance and size. Regional variations in mean size distribution, depth-related patterns and non-linear predator-prey dynamics emphasise the role of local environmental conditions in regulating the *A. aurita* medusa population during the spring post-strobilation phase.

Key words: Environmental drivers, Generalised Additive Models, medusae biological characteristics

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Introduction

The scyphozoan moon jellyfish (*Aurelia aurita* Linnaeus, 1758) is a globally distributed species that is commonly found in temperate and tropical waters (Lucas 2001). This species exhibits high adaptability and thrives under various oceanic conditions, including temperatures ranging from 4 to 31 °C, salinity levels between 5 and 38‰ and the ability to withstand hypoxic environments (Lucas 2001; Ishii et al. 2008; Sokołowski et al. 2016; Pinnow et al. 2023). The biphasic life cycle of *A. aurita*, comprising free-living pelagic medusae and sessile benthic polyps and reproductive strategies involving sexual and asexual reproduction, contribute to high population variability (Hansson 1997; Schiariti

et al. 2015; Pinnow et al. 2023). Moon jellyfish primarily feed on small zooplankton and can regulate zooplankton populations, thereby influencing the pelagic community structure (Behrends and Schneider 1995; Ramirez-Romero et al. 2018). Competition amongst zooplanktivorous species can affect small pelagic fish, particularly in ecosystems that are highly productive and subject to overfishing (Daskalov et al. 2007; Schnedler-Meyer et al. 2016).

The *A. aurita* population in the Black Sea has undergone substantial long-term fluctuations. Following a period of low total biomass in the 1940s and the 1950s, population biomass surged to 222–400 million tonnes in the 1980s. This increase has been attributed to heightened eutrophication, excessive fishing and a decline in mackerel stock, their primary predator (Gomou and Kupriyanov 1980; Zaitzev and Polishtuk 1984; Shushkina and Arnautov 1985; Zaitsev and Mamaev 1997). In the 1990s, the invasive development of the ctenophore *Mnemiopsis leidyi* led to a decline in *A. aurita* biomass to 36–100 million tonnes (Mutlu et al. 1994). The introduction of another non-native ctenophore, *Beroe ovata*, in 1997 (Konsulov and Kamburska 1998) preying on *M. leidyi*, led to new changes in the pelagic community (Niermann 2004; Shiganova et al. 2004; Oguz et al. 2008). Since the latter half of the 2000s, an increase in the *A. aurita* population has been observed (Bat et al. 2009) and high jellyfish bycatch has been recorded in pelagic trawlers (Özdemir et al. 2014). In 2013, jellyfish biomass along Crimea reached high levels, indicating *A. aurita* recovery due to the reduced presence of *M. leidyi* (Datsyk et al. 2016).

Significant seasonal variations have been observed in the *A. aurita* population in the Black Sea, with two annual medusa generations identified (Bat et al. 2009). The winter generation develops over approximately ten months, beginning in October/November, whereas the spring generation commences in March and April. Previous research has emphasised the importance of hydrographic factors in determining the distribution of *A. aurita* in the Black Sea (Kideys and Romanova 2001; Mutlu 2001). However, limited data exist on the changes in the biological characteristics of *A. aurita* in the western and north-western regions, particularly during periods of reduced predation pressure from the invasive ctenophore *M. leidyi*. To address this gap, we aimed to elucidate the ecological drivers governing the spring dynamics of *A. aurita* medusa population in these regions. Using observational data from spring surveys (2009–2015), we assessed the influence of environmental variables, including sea surface temperature and salinity, mesozooplankton quantity and abiotic factors (depth and region), on the key biological traits of *A. aurita* (mean bell diameter, abundance and biomass). Generalised Additive Models were employed to quantify non-linear relationships between predictors and jellyfish dynamics and to identify critical factors regulating the jellyfish medusa population during the post-strobilation phase.

Materials and method

Sampling strategy, samples collection and processing

Sampling was conducted in the western (WBS, Regions A and B, Fig. 1) and north-western parts of the Black Sea (NWBS, Region C) during the spring months (May-June) between 2009 and 2015.

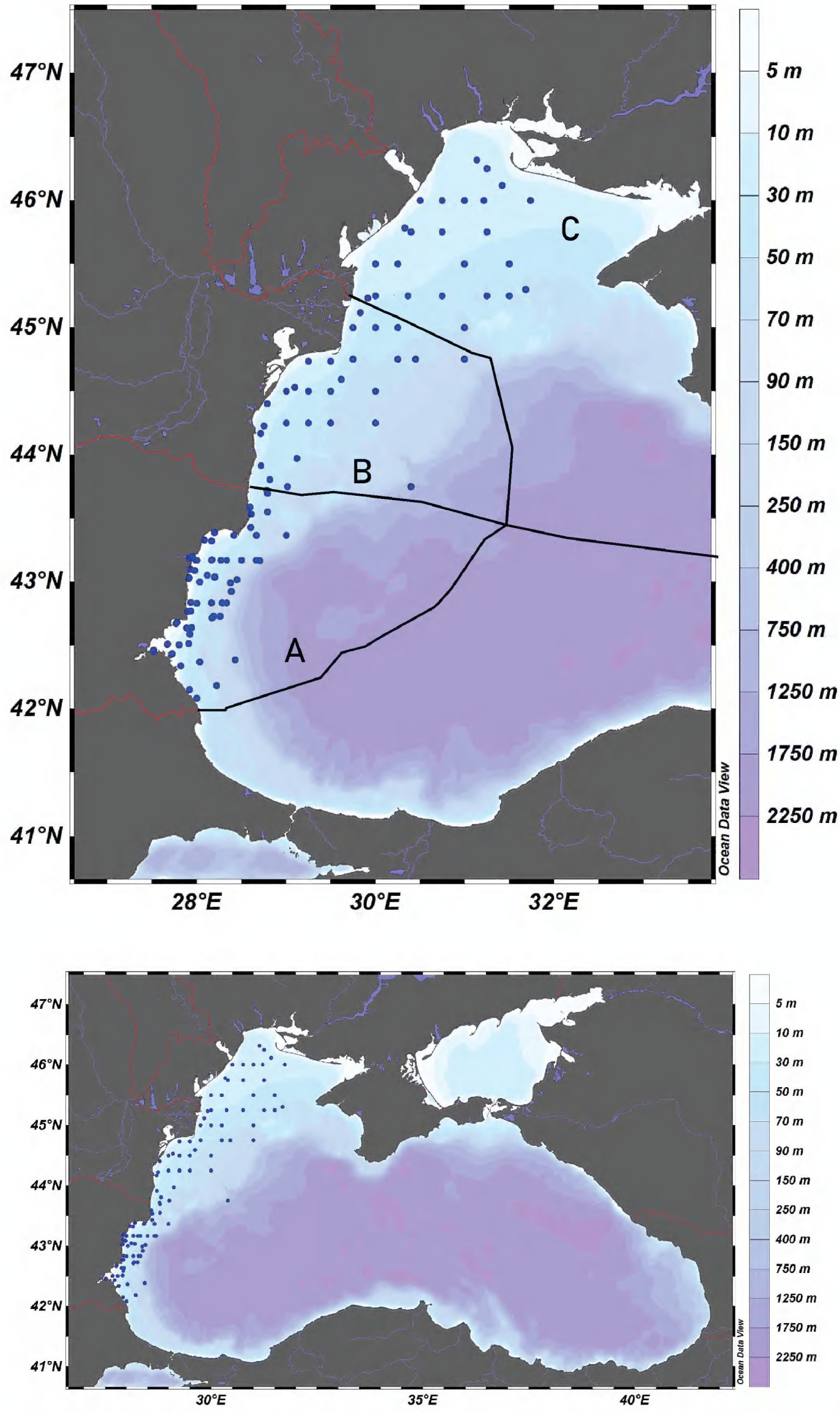

Figure 1. Map of the studied Exclusive Economic Zones in the Black Sea during May-June 2009–2015. (A: Bulgarian waters; B: Romanian waters; C: Ukrainian waters. The dots indicate unique geographic locations, with overlapping stations consolidated into single points on the map).

The geomorphology of the study region is defined by a gently sloping continental shelf extending 150–200 km offshore (Oguz 2019). The north-western shelf is broad (~ 200 km) and shallow with a mean depth of ~ 50 m. In contrast, the

western region exhibits a narrower shelf and deeper waters owing to a steep continental slope. Circulation patterns are dominated by the cyclonic Rim Current, which flows along the basin periphery, whereas local anticyclonic gyres enhance nutrient retention and sustain elevated biological productivity (Oguz and Besiktepe 1999). The study area is heavily influenced by major riverine inflow (e.g. Danube, Dniester and Dnieper) that supplies large volumes of nutrient-rich freshwater and organic matter. These discharges reduce the surface salinity and stimulate primary production (Yunev et al. 2022). Seasonal surface warming during spring further amplifies vertical stratification, as shallow waters heat more rapidly than deeper layers (Oguz 2019). The interplay of geomorphological and hydrological processes creates a complex and dynamic environment in the western and north-western Black Sea with high variability in plankton communities.

This study included 216 sampling stations, predominantly located in coastal and shelf waters, with stations in Bulgarian and Romanian waters also encompassing the continental slope at a maximum depth of 170 m (Table 1, Fig. 1). The main depth strata sampled were categorised as follows: (1) < 25 m, (2) 25–50 m, (3) 50–75 m and (4) greater than 75 m. It is worth mentioning that, in the Ukrainian sector (Region C), only two depth strata (up to 50 m) were sampled because of the shallow depths in the area.

Table 1. Distribution of *A. aurita* sampling stations by region, bottom depth and year of observation (the percentage share of sampling stations was calculated separately for each variable).

Variable	Categories	N of Samples	%
Region	(A) Bulgarian sector	162	75.000
	(B) Romanian sector	30	13.889
	(C) Ukraine sector	24	11.111
Depth	(1) < 25 m	98	45.370
	(2) 25–50 m	81	37.500
	(3) 50–75 m	18	8.333
	(4) > 75 m	19	8.796
Year	2009	52	24.074
	2010	27	12.500
	2011	10	4.630
	2012	53	24.537
	2013	24	11.111
	2014	34	15.741
	2015	16	7.407

The moon jellyfish was collected using a Bongo net, consisting of paired rings with an opening diameter of 0.6 m and net mesh sizes of 300 μm and 500 μm. A weight of 20 kg was attached to the net to stabilise its movement. Sampling was conducted using the oblique tow method, at a towing speed of 1–2 knots. The net was equipped with a flow meter to measure the volume of the filtered water. After sample collection, gelatinous zooplankton was sorted by species and the abundance, linear size and biovolume of moon jellyfish were determined. The umbrella diameter of fresh jellyfish was measured with a precision of 0.1 cm. The number of jellyfish per cubic metre was calculated using the following formula:

$$N\ (ind/m^3) = N\ sample/V\ filtered\ water$$

where N is the total number of jellyfish individuals in the Bongo net sample and V is the volume of filtered water, estimated from the flow meter data. The same formula was used to estimate the jellyfish biomass, based on the biovolume of each *A. aurita* sample. Details of the sampling methodology and calculations were provided by Shiganova et al. (2021).

Mesozooplankton samples were collected through vertical hauls using a Juday plankton net (equipped with a flowmeter) with a 36 cm diameter opening and 150 µm mesh size. Two distinct sampling methodologies were employed to balance the collection of jellyfish with that of potential prey. The Bongo net, characterised by a larger mesh size, is effective for macrozooplankton collection, but inadequate for capturing smaller mesozooplankton and their developmental stages. In contrast, the Juday net effectively sampled small-sized mesozooplankton communities throughout the water column. The mesozooplankton samples were preserved in 4% formaldehyde and processed as described by Alexandrov et al. (2020). Mihneva and Stefanova (2013) provided detailed descriptions of laboratory processing techniques. Species abundance was measured as ind/m^3, whereas biomass was estimated as mg/m^3 using species weights, according to Alexandrov et al. (2020).

Simultaneously with the zooplankton sampling, water temperature and salinity data were obtained using a Seabird Electronics CTD 32 carousel.

Statistical analysis

A Generalised Additive Model (GAM), a flexible regression technique that considers non-linear relationships between the dependent and independent variables, was employed for the analysis. This approach enables the creation of conceptual diagrams by plotting the dependent variable against independent variables and generating a curve that describes the data points. The GAM result is ecologically sound as it allows empirical data to dictate the shape of the resulting curve, ensuring that the model accurately reflects the natural variability and complexity of ecological relationships (Zuur et al. 2009; Higdon 2013; Wood 2017).

Before modelling, the data on *A. aurita* biomass (AB), abundance (AA) and data for predictors such as mesozooplankton biomass (MZB) and abundance (MZA) were square root transformed to stabilise the variance, which improved model fit and interpretability.

Three separate GAMs were used to examine the associations between the response variables (*A. aurita* abundance, biomass and mean size) and predictor variables (sea surface temperature (SST), sea surface salinity (SSS), mesozooplankton abundance and biomass, bottom depth and regions). The GAMs are expressed as:

$$Yi = \alpha. + s(Xi) + \varepsilon,$$ where (Yi) denotes the response variable (abundance, biomass or mean size), (α) is the intercept, (s(Xi)) is the smooth function of the predictor variables and (ε) is the error term.

The models were developed using XLSTAT software (Version 2023.3.0, Addinsoft) integrated with the R package mgcv. Predictor variables were selected through a backward stepwise elimination process, based on the Akaike Information Criterion (AIC), emphasising model parsimony and minimising overfitting. While variables with p-values < 0.05 were included in the final model, AIC primarily

guided the selection. Model performance was evaluated using the adjusted R^2 and the percentage of deviance explained. Smoothing parameters were determined via Generalised Cross-Validation (GCV) to balance the goodness-of-fit and smoothness, thereby mitigating overfitting. Model validity was evaluated using tests for homogeneity (residuals vs. fitted values), independence (residuals vs. explanatory variables), and normality (histograms and Q-Q plots).

Results

Environmental conditions

Analysis of the examined regions in the Black Sea revealed a range of differences in sea surface temperature (SST) and sea surface salinity (SSS), with averages of 18.97 °C (± 3.72 SD) and 15.52‰ (± 2.23 SD), respectively (Table 2). Nonetheless, the observed variability was consistent with earlier data (Shapiro et al. 2010). The average abundance of mesozooplankton was 2809.29 ind/m^3 (± 1914.71 SD), with a biomass of 51.59 mg/m^3 (± 30.48 SD), suggesting moderate productivity throughout the regions during this study (Table 2).

In spring, there was a consistent pattern of change in both sea surface temperature and salinity as the water depth increased. Specifically, the SST increased in coastal waters (Fig. 2A), whereas the SSS decreased near the shore (Fig. 2B), with the lowest SSS (7.85‰) in the vicinity of the Danube Delta. Conversely, higher surface salinity was recorded in Bulgarian waters (Fig. 2B).

The average mesozooplankton abundance and biomass were the lowest in the Ukrainian sector (1281.28 ind/m^3 and 19.63 mg/m^3) and the highest along the Bulgarian coast (3225.97 ind/m^3 and 59.46 mg/m^3). Peak mesozooplankton abundance typically occurred at depths up to 50 m, but a secondary increase in the Romanian waters was noted beyond 75 m (Fig. 2C). The mesozooplankton biomass showed a bimodal distribution in both Bulgarian and Romanian waters, with higher levels at depths of less than 25 m and over 75 m (Fig. 2D).

Table 2. Environmental variables: SST (°C), SSS (‰), MZA (ind/m^3), MZB (mg/m^3) per observed region and average levels (with standard deviations) for all regions.

Region		Variable	Minimum	Maximum	Mean	SD
All regions		SST	11.39	25.23	18.97	3.72
		SSS	7.85	18.20	15.52	2.23
		MZA	21.89	8151.93	2809.29	1914.71
		MZB	6.66	146.12	51.59	30.48
Western BS	Region A Bulgarian sector	SST	12.73	25.230	20.271	3.17
		SSS	10.117	18.200	15.991	1.674
		MZA	607.257	8151.931	3225.974	2018.99
		MZB	17.806	146.115	59.468	30.91
	Region B Romanian sector	SST	13.347	17.977	15.481	1.36
		SSS	7.847	17.940	12.646	3.551
		MZA	1106.457	5375.136	2148.314	1121.94
		MZB	20.858	74.738	40.525	14.57
North-western BS	Region C Ukrainian sector	SST	11.386	16.820	13.915	1.32
		SSS	12.727	18.143	15.347	1.844
		MZA	21.893	2852.702	1281.275	645.19
		MZB	6.656	43.793	19.625	8.69

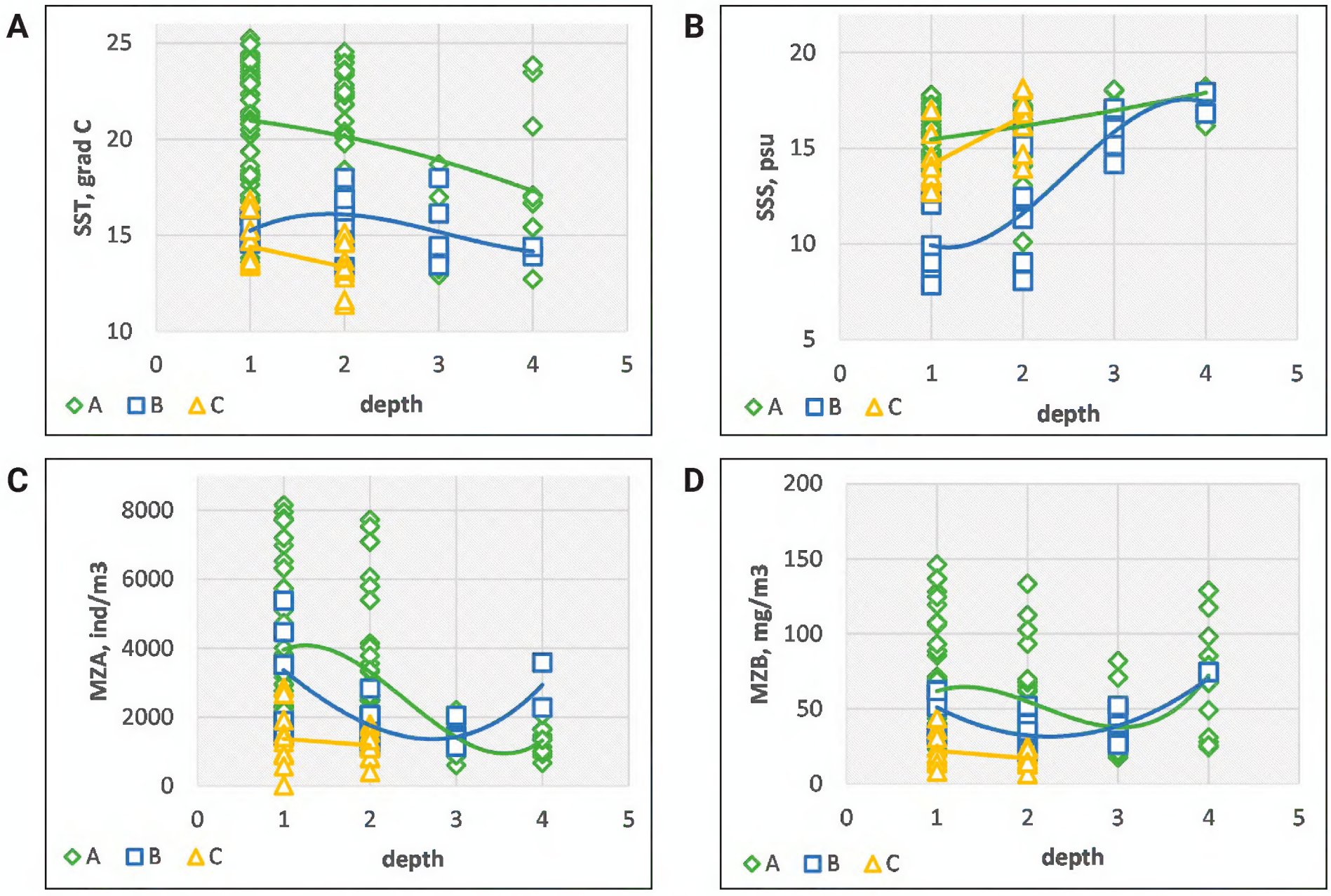

Figure 2. Environmental variables: SST (**A**), SSS (**B**), MZA (**C**) and MZB (**D**) by sampling depth ((1) < 25 m, (2) 25–50 m, (3) 50–75 m and (4) > 75 m) and region (A-Bulgarian, B-Romanian and C-Ukrainian sectors). The trend lines represent fourth-order polynomial regressions of the given variable fitted individually for different regions and across various depths.

Spring variability of *A. aurita* abundance (AA), biomass (AB) and mean size (AMS)

The data showed a maximum moon jellyfish abundance of 3.84 ind/m^3 and an average value of 1.44 ind/m^3 (±1.07 SD). *A. aurita* biomass ranges from 0 to 15.37 g/m^3, averaging 3.91 g/m^3 (± 3.82 SD). Average size ranges from 2.0 to 10.2 cm, with a mean value of 6.1 (± 1.7 SD) (Table 3). The Bulgarian sector (region A) demonstrates consistent trends in jellyfish abundance and biomass, with slightly lower mean values of 1.31 ind/m^3 (± 1.01 SD) and 3.79 g/m^3 (± 3.93 SD), respectively. The mean size was 6.2 cm (± 1.8 SD), indicating that, while the number of individuals was lower, they were, on average, larger in this region. Region B (Romania) had similar abundance (1.33 ind/m^3 ± 1.08 SD), biomass (3.99 g/m^3 ± 3.72 SD) and mean size (6.3 cm ± 1.7 SD). Region C (Ukraine) had the highest average abundance (2.48 ind/m^3 ± 0.92 SD) and biomass (4.65 g/m^3 ± 3.22 SD), but the smallest mean size (5.7 cm ± 1.5 SD).

Jellyfish abundance and biomass generally increased in the nearshore zone up to a depth of 25 m (Fig. 3A, B). However, in Romanian waters, a second peak of abundance was observed at depths of 50–75 m, whereas in the Bulgarian sector, jellyfish biomass appeared to slightly increase again at depths beyond 75 m. The mean size of moon jellyfish exhibited varying trends in the study regions (Fig. 3C).

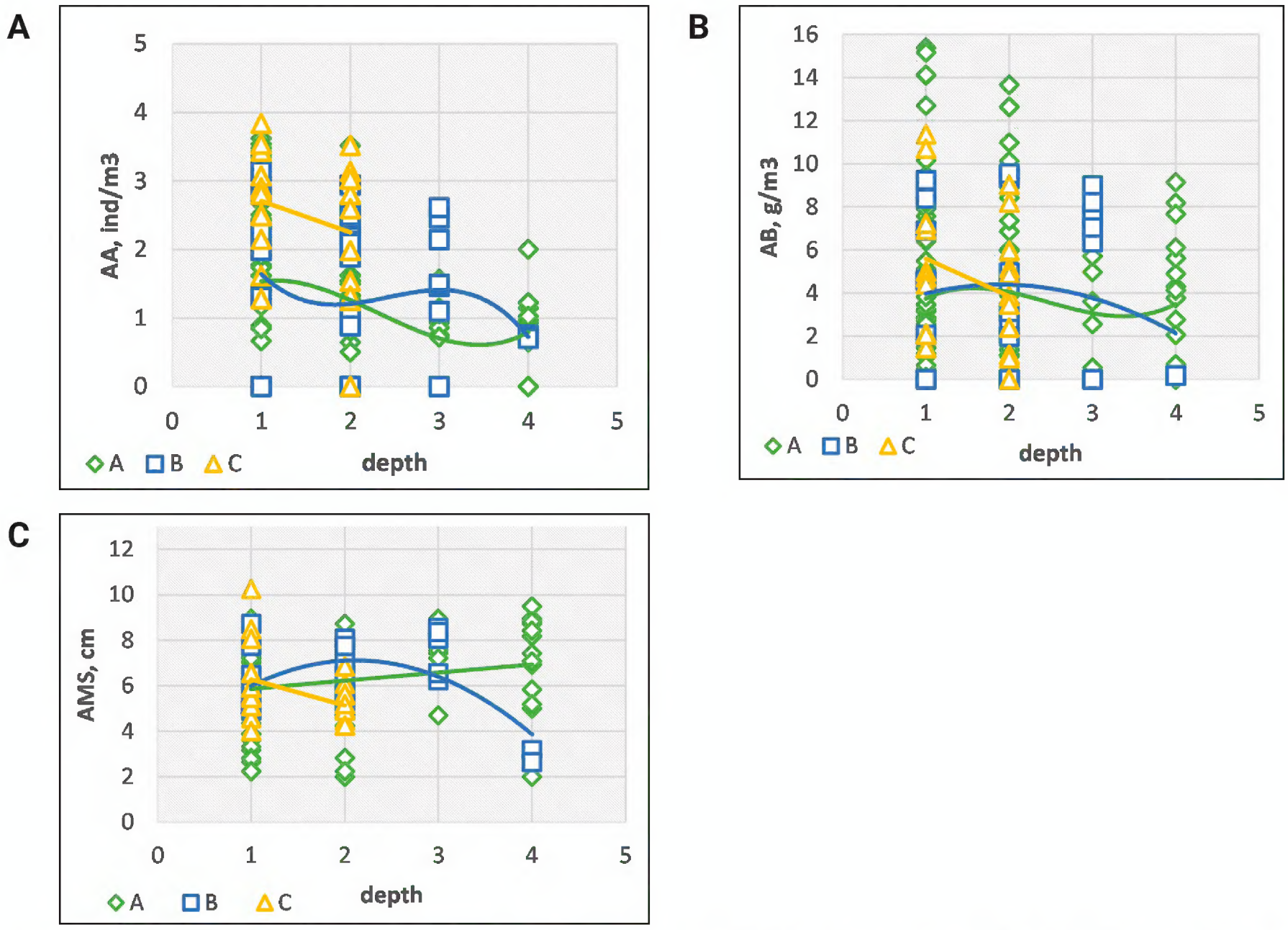

Figure 3. Variability in *A. aurita* abundance (AA, **A**), biomass (AB, **B**) and mean size (AMS, **C**) by sampling depth ((1) < 25 m, (2) 25–50 m, (3) 50–75 m and (4) > 75 m) and region (A-Bulgarian, B-Romanian and C-Ukrainian sectors). The trend lines represent fourth-order polynomial regressions of the given variable fitted individually for different regions and across various depths.

Table 3. Spring variability of *A. aurita* abundance (AA, ind/m^3), biomass (AB, g/m^3) and mean size (AMS, cm) in the observed regions.

Region		Variable	Maximum	Mean	SD
All regions		AA	3.84	1.44	1.07
		AB	15.37	3.91	3.82
		AMS	10.20	6.1	1.7
Western BS	Region A Bulgarian sector	AA	3.62	1.31	1.01
		AB	15.37	3.79	3.93
		AMS	9.50	6.2	1.8
	Region B Romanian sector	AA	3.14	1.33	1.08
		AB	9.54	3.99	3.72
		AMS	8.70	6.3	1.7
North-western BS	Region C Ukrainian sector	AA	3.84	2.48	0.92
		AB	11.38	4.65	3.22
		AMS	10.20	5.7	1.5

Modelling of *A. aurita* biomass, abundance and average size

GAM of *A. aurita* biomass

The GAM of *A. aurita* biomass explained 78.5% of its variation, indicating high explanatory potential. The significant predictors of *A. aurita* biomass included jellyfish mean size, mesozooplankton biomass (MZB) and sea surface salini-

ty (Table 4). However, SST, mesozooplankton abundance, "region" and "depth" did not exert significant effects on jellyfish biomass. Amongst the smoothed variables, jellyfish mean size had the most substantial influence on biomass, followed by sea surface salinity and mesozooplankton biomass (Table 4). The biomass of *A. aurita* increased with increasing jellyfish size up to an average disc diameter of ~ 8 cm (Fig. 4). Elevated jellyfish biomass demonstrated an inverse relationship with SSS, reaching high values at salinities of 8–12‰ and a second, but smaller increase at salinities of approximately 16–17‰, typical of the plume of transformed Danube waters. Mesozooplankton biomass has emerged as a notable predictor with non-linear effects on *A. aurita* biomass. The peak *A. aurita* biomass corresponded to the lowest MZB levels, indicating the potential for MZB regulation. However, when MZB was increased to 100 mg/m^3, *A. aurita* biomass exhibited an upward trend, with a direct positive relationship between the two variables.

Table 4. GAM results for *A. aurita* biomass, including parametric coefficients (intercept) and smooth terms (average medusa size (AMS), mesozooplankton biomass (MZB) and sea surface salinity (SSS)) with effective degrees of freedom (edf), F-statistics and significance levels (p-values).

	Estimate	**Std. Error**	**t value**	**Pr(> |t|)**
(Intercept)	2.057	0.038	53.757	0.000
	edf	Ref.df	F	p-value
s(AMS)	4.208	5.169	61.479	0.000
s(MZB)	2.622	3.267	4.833	0.003
s(SSS)	5.215	6.045	5.830	0.000

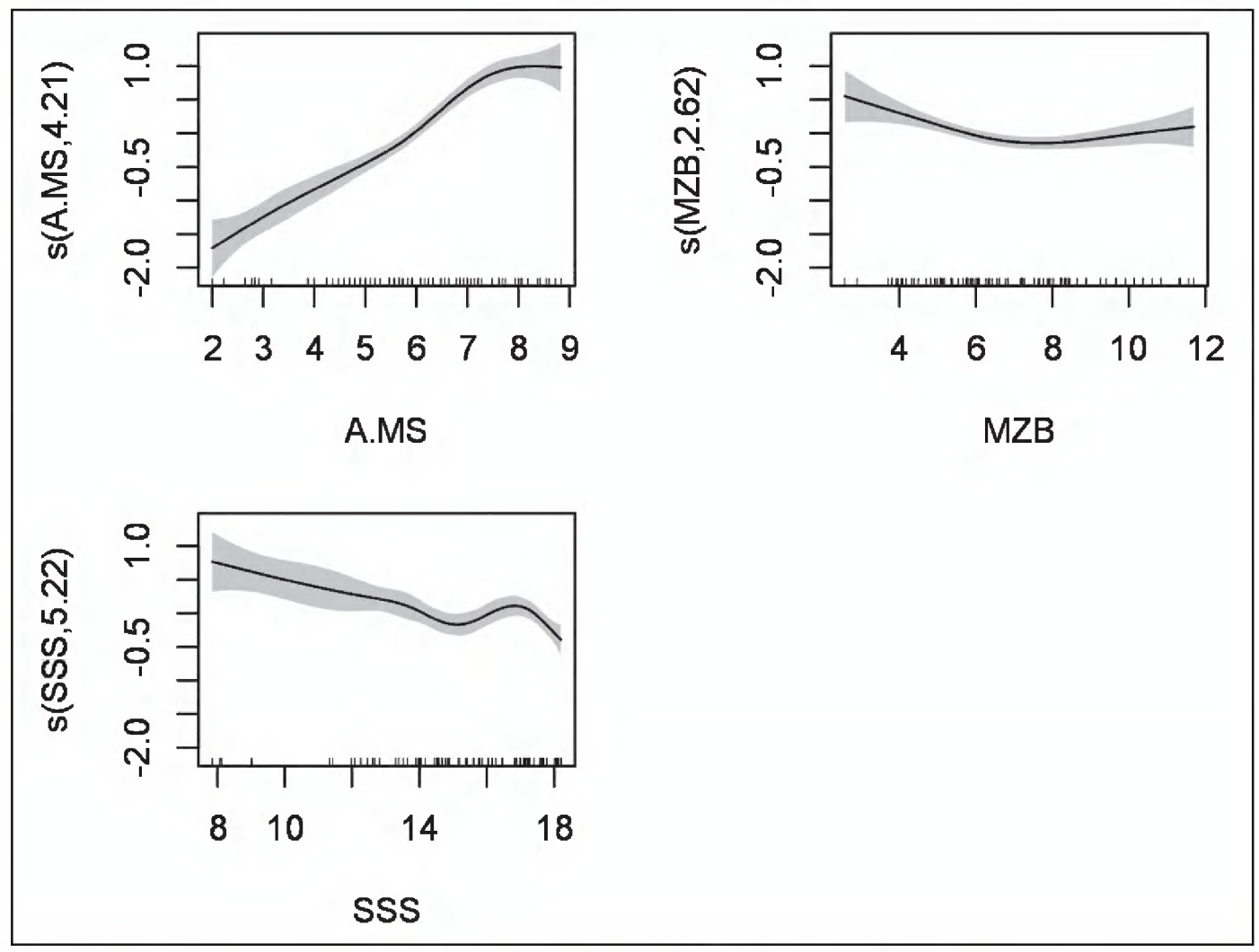

Figure 4. Contribution of the factors *A. aurita* mean size (AMS, cm), mesozooplankton biomass (MZB, mg/m^3, square root-transformed) and sea surface salinity (SSS, ‰) to the modelled *A. aurita* biomass ((g/m^3, square root-transformed).

GAM of *A. aurita* abundance

The GAM of *A. aurita* abundance explained 44.8% of the variance, suggesting moderate explanatory power. The intercept coefficient is highly significant ($p < 0.001$) and, amongst the smoothed terms, depth, mesozooplankton biomass and *A. aurita* mean size are crucial predictors of jellyfish abundance (Table 5).

The relationship between the abundance of *A. aurita* and mesozooplankton biomass mirrored the relationship between jellyfish biomass and MZB, with pronounced non-linear effects (Fig. 5). At lower MZB levels, an inverse relationship was observed, indicating that *A. aurita* may regulate the mesozooplankton biomass. However, an increase in MZB above ~ 100 mg/m^3 corresponds to an increase in jellyfish density. The influence of depth on jellyfish abundance was pronounced, with maximum quantities observed at depths less than 50 m. Jellyfish abundance increased with increasing mean size up to 8 cm; however, larger mean sizes may be associated with a slight reduction in abundance.

Table 5. GAM results for *A. aurita* abundance with estimated parametric coefficients (intercept) and smoothed terms (average medusa size (AMS), mesozooplankton biomass (MZB), depth) with effective degrees of freedom (edf), F-statistics and significance levels (p-values).

	Estimate	**Std. Error**	**t value**	**Pr(> |t|)**
(Intercept)	1.354	0.020	67.751	0.000
	edf	Ref.df	F	p-value
s(AMS)	2.177	2.729	4.812	0.006
s(MZB)	2.407	3.002	4.513	0.005
s(depth)	1.740	2.171	26.348	0.000

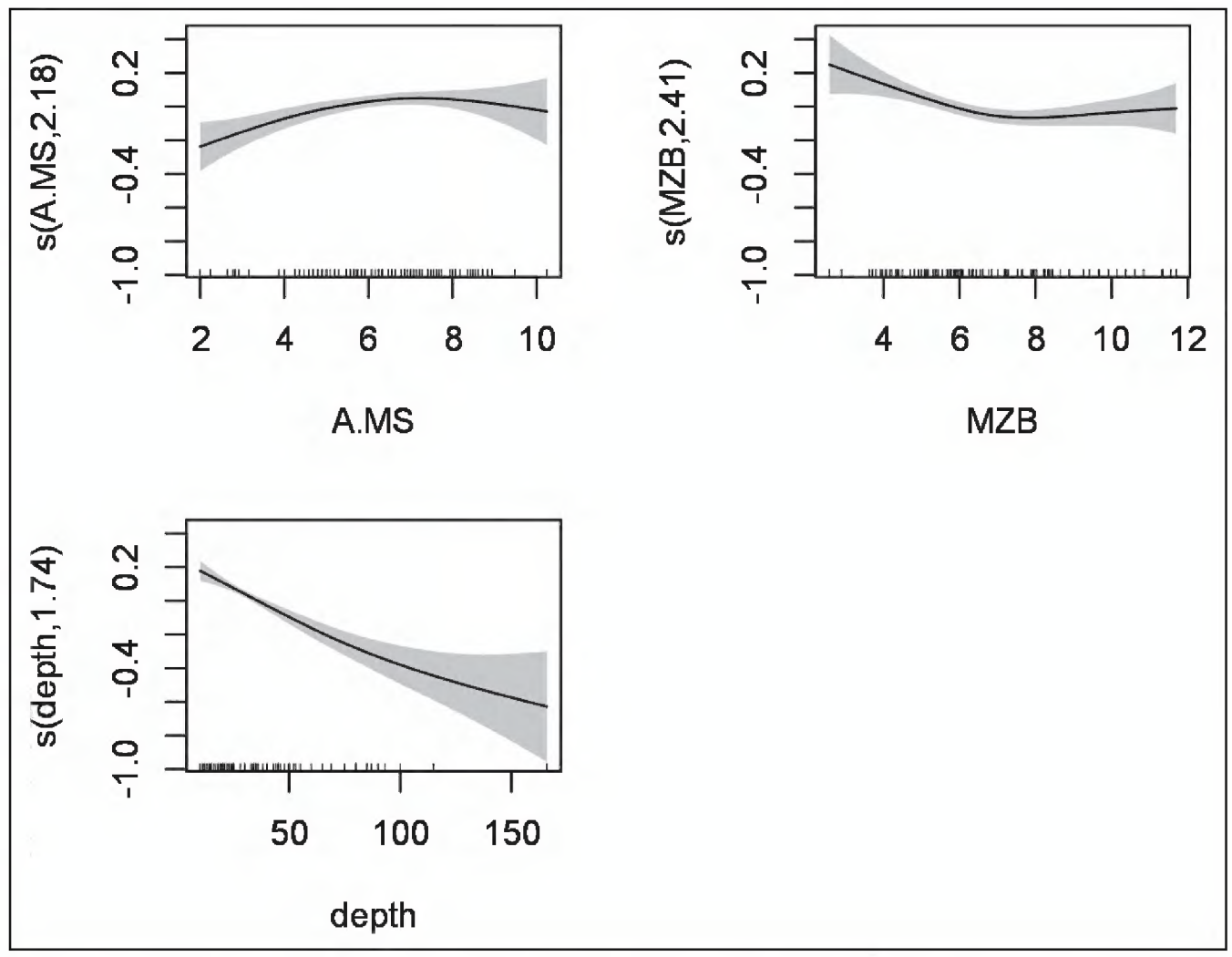

Figure 5. Contribution of the factors *A. aurita* mean size (AMS, cm), mesozooplankton biomass (MZB, mg/m^3, square root-transformed) and sampling depth (m) to the modelled *A. aurita* abundance (ind/m^3, square root-transformed).

GAM of *A. aurita* average size

The GAM assessment of the average size *of A. aurita* produced an adjusted R^2 value of 0.745, suggesting a good explanatory power (74.5%) (Table 6). The parametric coefficients revealed that the factor "region" significantly influenced *A. aurita* average size, with north-western region demonstrating the highest size reduction compared to the reference region. The smoothed terms for *A. aurita* biomass (AB) and depth variables were also significant, with F-values of 99.303 ($p < 0.001$) for AB and 8.79 ($p < 0.001$) for depth, suggesting effects on the average size of *A. aurita*. Overall, a positive correlation was observed between jellyfish mean size, biomass and depth, with jellyfish size increasing with depth, particularly over 50 m (Fig. 6).

Table 6. GAM output for *A. aurita* average size in the north-western and western Black Sea, showing estimated parametric coefficients (intercept, regional contrasts (B, C)) and smoothed terms (abundance (AB), depth) with effective degrees of freedom (edf), F-statistics and significance levels (p-values).

	Estimate	Std. Error	t value	Pr(> |t|)
(Intercept)	6.218	0.080	77.726	0.000
Region B	-0.461	0.211	-2.182	0.031
Region C	-0.866	0.205	-4.213	0.000
	edf	Ref.df	F	p-value
s(AB)	3.464	4.286	99.303	0.000
s(depth)	3.686	4.416	8.792	0.000

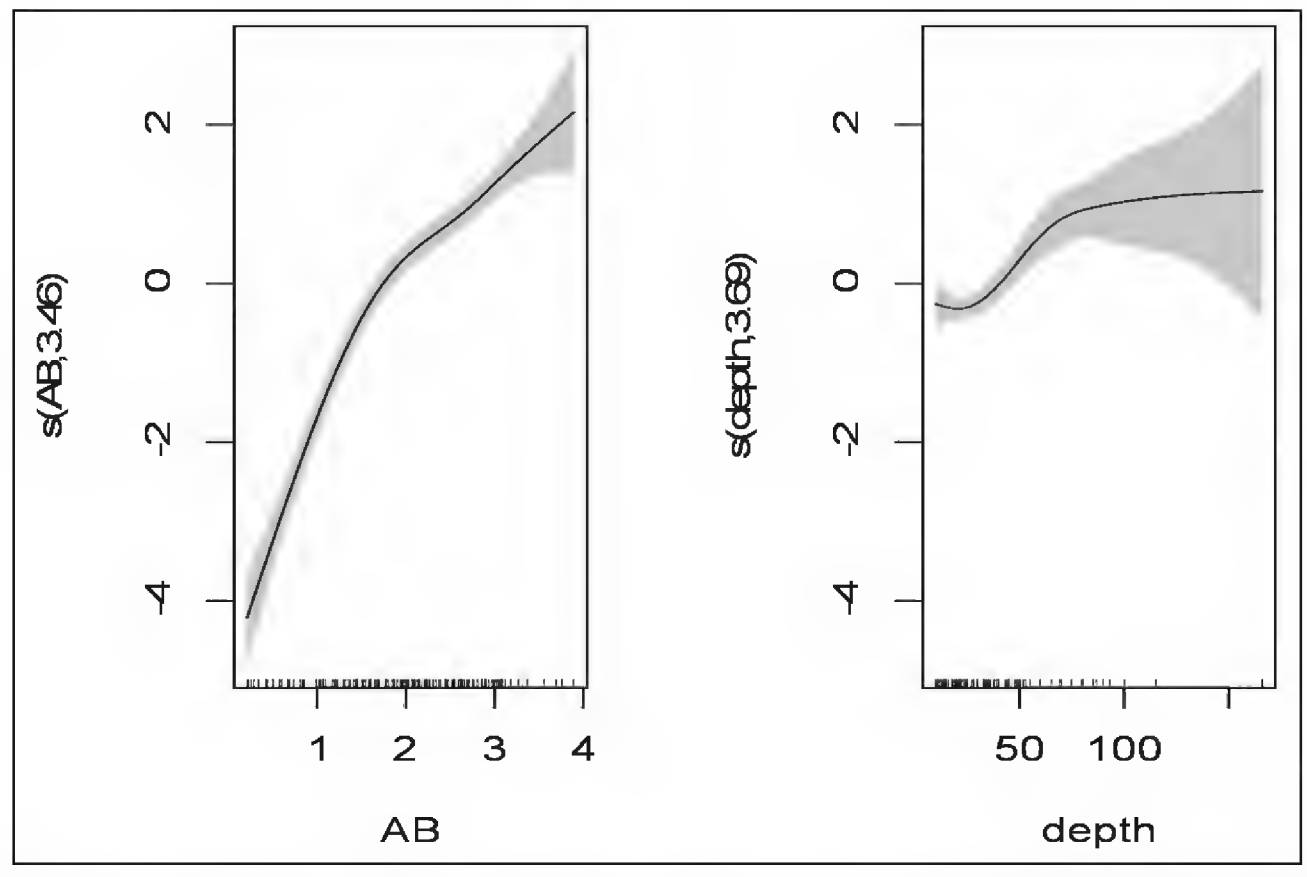

Figure 6. Contribution of *A. aurita* biomass (AB, g/m^3, square root-transformed) and sampling depth (m) to the modelled *A. aurita* average size (cm).

Discussion

GAMs identified mesozooplankton biomass (MZB) and sea surface salinity (SSS) as the primary drivers of *A. aurita* biomass during spring. Jellyfish biomass exhibited a significant inverse relationship with salinity, peaking at low

salinities (8–12‰), likely mediated by nutrient-rich freshwater inflows from the Danube, Dniester and Dnieper Rivers. These discharges enhance primary productivity and plankton availability, particularly during the peak Danube discharge (8,000–9,000 m^3/s) in April–May (Kara et al. 2008; Yunev et al. 2022). A secondary smaller peak in jellyfish biomass at intermediate salinities of 16–17‰, aligns with the dispersal of the transformed Danube plume waters, highlighting that the north-western and western Black Sea shelves are optimal habitats for medusa biomass accumulation.

While mesozooplankton biomass (MZB) strongly predicted *A. aurita* biomass and density, it demonstrated no significant relationship with medusae size during the study period. The models described a non-linear relationship between *A. aurita* density and MZB, reflecting contrasting trophic controls. At high MZB (> 100 mg/m^3), jellyfish biomass increased, indicative of resource control, whereas another density peak at low MZB (< 20 mg/m^3) suggested suppression of zooplankton via jellyfish predation. However, size structure might also be governed by reproductive strategies and density-dependent competition (Schneider and Behrends 1994). Early spring asexual reproduction (strobilation) releases cohorts of small medusae into the population, causing size variability (Mihneva et al. 2009). Increased jellyfish density is known to intensify intraspecific competition, potentially influencing growth and average size, highlighting the role of density-dependent processes in shaping population structure (Schneider and Behrends 1994). Schneider and Behrends (1994) further demonstrated that, while high MZB enhances jellyfish biomass, competition during medusa-rich years can result in smaller sizes compared to medusa-poor years. Extreme food scarcity may also induce degrowth as a survival strategy (Ishii and Båmstedt 1998).

Our study revealed that *A. aurita* abundance increased in parallel with a mean size of up to 8 cm, but slightly declined when the mean size exceeded this range. This pattern aligns with the natural life cycle of the species, in which larger individuals from the overwintering population might experience post-reproductive mortality following gamete release. As noted by Lucas (2001), post-spawning medusae often undergo shrinkage and mortality owing to morphological degradation from gamete release.

The GAM highlighted significant regional differences in *A. aurita* size, with medusae on the north-western shelf exhibiting smaller mean bell diameters (5.7 cm) than those in the western regions (6.2–6.3 cm). These spatial differences are likely connected with local environmental gradients, including the shelf depth, food availability and hydrodynamic regimes. Depth emerged as a critical predictor, with shallower waters (< 50 m) supporting higher densities of smaller medusae, a pattern consistent with the post-strobilation phase, with coastal zones acting as post-strobilation nurseries near benthic polyp habitats. Hydrodynamic processes, such as wind-driven circulation (Oguz and Besiktepe 1999), combined with cryptic genetic diversity within the genus Aurelia (Ramsak et al. 2012) may further contribute to regional adaptations.

Sea surface temperature did not significantly predict *A. aurita* dynamics, potentially because the narrow sampling period (May–June) limited the evaluation of temperature effects, which are more apparent over broader seasonal cycles.

In conclusion, this study highlights the interplay of environmental drivers (salinity, depth), trophic interactions (mesozooplankton biomass) and potentially

intrapopulation mechanisms in shaping the spring dynamics of the *A. aurita* medusa stage. Regional effects on medusa mean size, coupled with depth-related distribution patterns and non-linear predator-prey dynamics, further emphasise the influence of localised environmental heterogeneity. The observed patterns reflect the post-strobilation phase, capturing the effects of asexual reproduction and demographic overlap between the overwintering and newly-formed spring populations. Further research should integrate a multifactor analysis of life history, hydrodynamic forcing and trophic dynamics to advance predictive models of jellyfish dynamics and their ecosystem impacts.

Conclusions

This study investigated the ecological drivers governing the spring dynamics of the *A. aurita* medusa stage in the western and north-western Black Sea. GAMs demonstrated high explanatory power for jellyfish biomass and mean size, accounting for 75–79% of the observed variation, indicating that the key drivers of these traits were effectively captured. In contrast, the GAM for *A. aurita* abundance explained 45% of the variance, emphasising both the influence of critical ecological factors and the inherent complexity of abundance dynamics. Mesozooplankton biomass and sea surface salinity emerged as key predictors of jellyfish biomass, with elevated biomass observed in low-salinity nutrient-rich zones influenced by river plumes. Although MZB exhibited non-linear relationships with jellyfish biomass, reflecting both food resource-driven increases and the predatory suppression of zooplankton, it had no significant effect on the medusa mean size during the study period. The latter suggests that medusae size structure is modulated by additional mechanisms, such as density-dependent competition and reproductive strategies (e.g. strobilation-driven recruitment of small medusae). Regional disparities in jellyfish size, depth-related distribution patterns and non-linear predator-prey interactions further emphasised the role of local environmental conditions in shaping the population structure. Future studies should integrate environmental variability with population-level processes to refine the predictive models of jellyfish dynamics and their ecological impacts.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

All of the data that support the findings of this study are available upon request.

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